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ARTICLE

RESEARCH ARTICLE

Operational use of mass-trapping to study and suppress *Monochamus galloprovincialis* (Col.: Cerambycidae) populations: a field case

Uso operativo de trampeo masivo para estudiar y reducir poblaciones de *Monochamus galloprovincialis* (Col.: Cerambycidae): un caso práctico

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Abstract: *Aim of the study*: To investigate mass trapping as a less invasive and cost-effective alternative to large-scale clear-cutting for controlling *Monochamus galloprovincialis* (Olivier, 1795), the primary vector of the pine wood nematode *Bursaphelenchus xylophilus* (Steiner & Buhrer, 1934) Nickle, 1970, the causal agent of pine wilt disease (PWD) in southern European coniferous forests. *Area of study*: Two field experiments were conducted in a 209 ha *Pinus pinaster* Aiton stand in Pino del Río (Palencia, Spain). Additionally, long-term PWD management was evaluated in the demarcated area of Sancti-Spiritus (Salamanca, Spain). *Material and methods*: Beetle population size was estimated using capture-mark-recapture (CMR) and analyzed with the Jolly-Seber model. Trapping efficiency at different trap densities was assessed using generalized linear models. Long-term disease management combined mass trapping with the removal of symptomatic trees over a 10-year period. *Main results*: Trap densities of 0.11, 0.44, and 1 trap/ha removed 19.3%, 67.4%, and 85% of the beetle population, respectively. Logistic regression predicted near-complete suppression at 1.8 traps/ha. In Sancti-Spiritus, after 10 years of integrated management, no positive results were found in plant or insect vector samples, and the disease was considered eradicated from the demarcated area. *Research highlights*: Mass trapping is a viable alternative or complement to clear-cutting in PWD management, particularly in high-risk areas where terrain complexity or forest stand conditions hinder effective tree and debris removal.

Keywords: *Bursaphelenchus xylophilus*; capture-mark-recapture; Jolly-Seber; mass-trapping; pheromone traps; pine wilt disease; population dynamics.

Resumen: *Objetivo del estudio*: Investigar el trampeo masivo como una alternativa menos invasiva y rentable a la tala rasa a gran escala para el control de *Monochamus galloprovincialis* (Olivier, 1795), vector principal del nematodo de la madera del pino *Bursaphelenchus xylophilus* (Steiner & Buhrer, 1934) Nickle, 1970, agente causal de la enfermedad del marchitamiento de los pinos en los bosques de coníferas del sur de Europa. *Área de estudio*: Se realizaron dos experimentos de campo en un pinar de *Pinus pinaster* Aiton de 209 ha en Pino del Río (Palencia, España). Además, se evaluó el manejo a largo plazo de la enfermedad en el área delimitada de Sancti-Spiritus (Salamanca, España). *Material y métodos*: El tamaño de la población de escarabajos se estimó mediante captura-marcaje-recaptura (CMR) y se analizó con el modelo de Jolly-Seber. La eficiencia del trampeo a diferentes densidades de trampas se evaluó mediante modelos lineales generalizados. El manejo a largo plazo de la enfermedad combinó el trampeo masivo con la eliminación de árboles sintomáticos durante un período de 10 años. *Resultados principales*: Densidades de trampas de 0,11, 0,44 y 1 trampa/ha eliminaron el 19,3%, el 67,4% y el 85% de la población de escarabajos, respectivamente. La regresión logística predijo una supresión casi completa con 1,8 trampas/ha. En Sancti-Spiritus, después de 10 años de manejo integrado, no se encontraron resultados positivos en muestras vegetales ni de insectos vectores, y la enfermedad se consideró erradicada del área delimitada. *Aspectos destacados de la investigación*: El trampeo masivo y la eliminación de árboles sintomáticos es una estrategia eficaz y viable para el manejo del vector en áreas donde la tala es difícil o contraproducente.

Palabras clave: *Bursaphelenchus xylophilus;* captura-marcado-recaptura; captura masiva; dinámica de población; enfermedad del marchitamiento del pino; Jolly-Seber; trampas de feromonas.

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Supplementary information ↓

1. INTRODUCTION

The pine wood nematode (PWN) *Bursaphelenchus xylophilus* (Steiner & Buhrer, 1934) Nickle, 1970 is an agent of pine wilt disease (PWD) (Wingfield, 1982), a quarantine organism that has caused millions of dollars in losses worldwide since its first detection outside its natural distribution area at the beginning of the 20th century. Nematodes can move freely within wood and pass from one host material to another in direct contact (Wingfield & Blanchette, 1983); however, if they are not in contact, they require the help of a beetle of the genus *Monochamus* to transport and transmit it to new hosts through feeding and oviposition (Naves et al., 2007; Linit & Akbulut, 2008). On the Iberian Peninsula, the pine sawyer beetle *Monochamus galloprovincialis* (Olivier, 1795) (Coleoptera: Cerambycidae) does not cause significant damage to trees because it is a secondary decomposer of fallen or even recently dead trees (Vives & Ramos, 2000). However, it has reached great importance as a pest in Europe since the introduction of PWD in Portugal. The spread of PWD is considered a serious risk to coniferous forests in the warm and dry pine forests of southern Europe (Evans et al., 1996). The development of effective trapping devices, such as modified multiple-funnel (Álvarez et al., 2016) or cross-vane traps, which are well suited for the capture of *M. galloprovincialis,* and the improvement of a very attractive lure for *Monochamus* spp. (Pajares et al., 2004) raised the possibility of controlling the disease by using its vector.

According to the Commission Implementing Decision of February 13, 2006 (European Commission, 2006) in the event of nematode detection in new areas, Member States must adopt eradication measures, including the preventive felling of susceptible plants in the infested area within a variable radius. With these instructions, the first outbreak was detected in Spain in 2008 in Villanueva de la Sierra, Cáceres (Consejería de Agricultura y Desarrollo Rural, 2008a) and was subsequently eradicated after cutting down all the pines present in an area of 3 km radius around the infected tree, a hard measure taken by the regional government on the recommendation of the European Commission (Consejería de Agricultura y Desarrollo Rural, 2008b). Since then, another six outbreaks have occurred in Spanish territory, generally close to the Portuguese border: As Neves (Pontevedra, 2010), Valverde del Fresno (Cáceres, 2012, eradicated in 2017), Sancti-Spiritus (Salamanca, 2013, eradicated in 2018), Lagunilla (Salamanca, 2018), Malvana (Cáceres, 2019) and Lobios (Ourense, 2024). Four of them are active, three are under eradication measures and one is under contention measures.

As the occurrence of PWD is strongly affected by vector density, monitoring of adults could be decisive. Yoshimura et al. (1999) reported a model to predict how the spread of disease could be controlled by removal of pine sawyers concluding that the disease fails in invasion when beetles' density is very low due to the Allee effect. Torres-Vila et al. (2014) and Sánchez-Husillos et al. (2015) investigated the prospects of using traps to reduce *M. galloprovincialis* populations. However, only the latter study achieved positive results, with trap densities of 0.02, 0.11, 0.25, and 0.44 traps/ha removing 4.66%, 20.50%, 33.33%, and 59.80% of a high population density, respectively, indicating that 95% of the population would be removed at 0.82 traps/ha. The practical information provided by Sánchez-Husillos et al. (2015) was used as a reference after the outbreak declared in Sancti-Spiritus (Salamanca) in 2013. In the following years, nearby pine stands of the demarcated area were managed by mass trapping and wilted pine removal as part of the eradication measures contemplated in the Spanish contingency plan for pine wood nematode disease, as it was known that they consisted of high-density vector population stands. In this study, we report the results of this field experience of PWD management as an efficient alternative to clear-cutting for specific situations as well as the results of two experiments aimed at estimating population size and mass trapping efficiency at low-density *M. galloprovincialis* populations.

2. MATERIAL AND METHODS

2.1. Mass-trapping assay and population size estimation

2.1.1. Study site

Both trials were conducted in a regular, continuous 209 ha, 60-year-old reforested *Pinus pinaster* Aiton stand located in Pino del Río (Palencia, Spain) (Figure 1). The study site was subdivided into two similar contiguous zones: the "population size estimation area", which covered 40 ha, and the "mass trapping area" consisting of 169 ha.

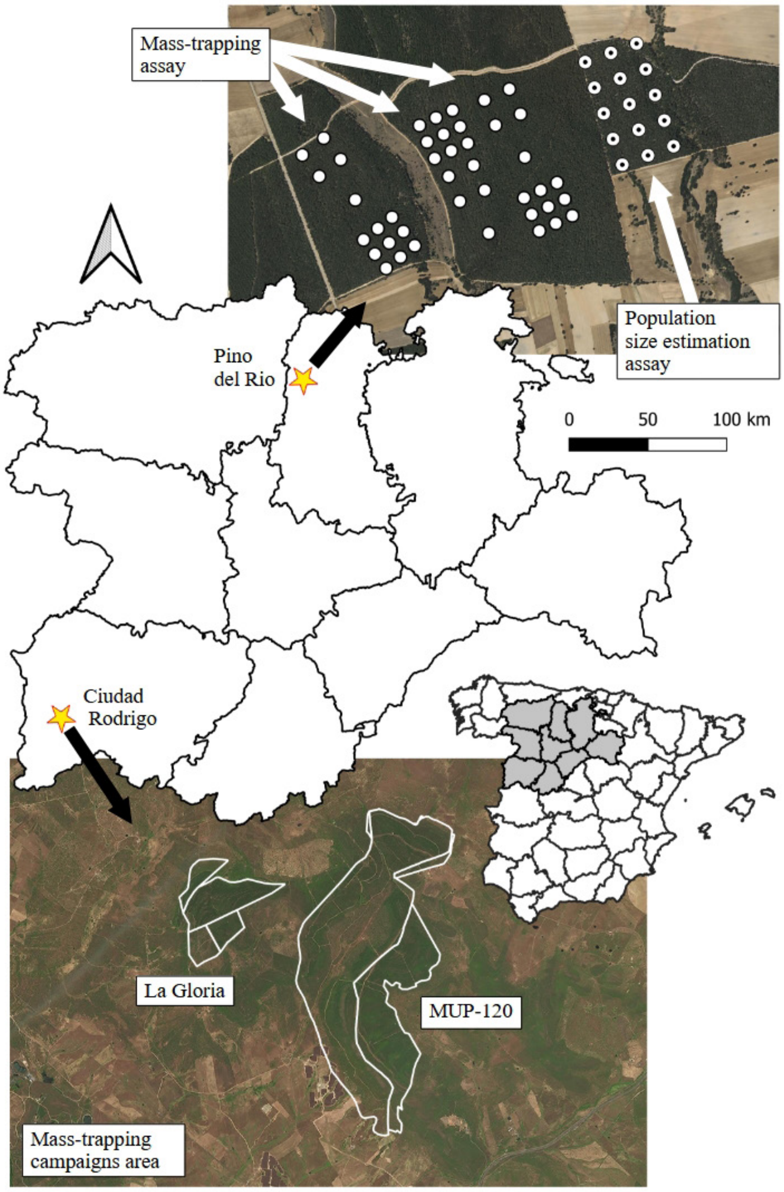

Figure 1. Location of both mass-trapping and population size estimation assays in Pino del Rio (Palencia, Spain) and La Gloria and MUP-120 forests stands in Ciudad Rodrigo (Salamanca, Spain).

2.1.2. Experimental design

Both trials were conducted simultaneously during the entire flight period of the insect vector between 13 June and 22 October, 2014. Twelve-funnel multi-funnel traps were used after be modified to prevent the escape of *M. galloprovincialis* by applying a Teflon® coating to the collection cup and the inner face of the lowest funnel (ECONEX S.L., Murcia, Spain; Álvarez et al. 2014). Traps were hung from ropes between trees with the collection cup placed at least 50 cm from the ground and baited with Galloprotect Plus® lures (SEDQ S. L., Barcelona, Spain) that were replaced every six weeks. To estimate the population size of *M. galloprovincialis*, a capture-mark-recapture (CMR) trial was conducted. Fifteen traps were placed in a regular grid, with a distance of 150 m between traps (0.44 traps/ha, Figure 2). The traps were checked weekly throughout the study period, and to promote the survival of captured adults, fresh pine twigs were periodically added to the collection container. All captured insects were identified using an indelible marker and were sexed to be released again between the trap where they had been captured and the next closest trap.

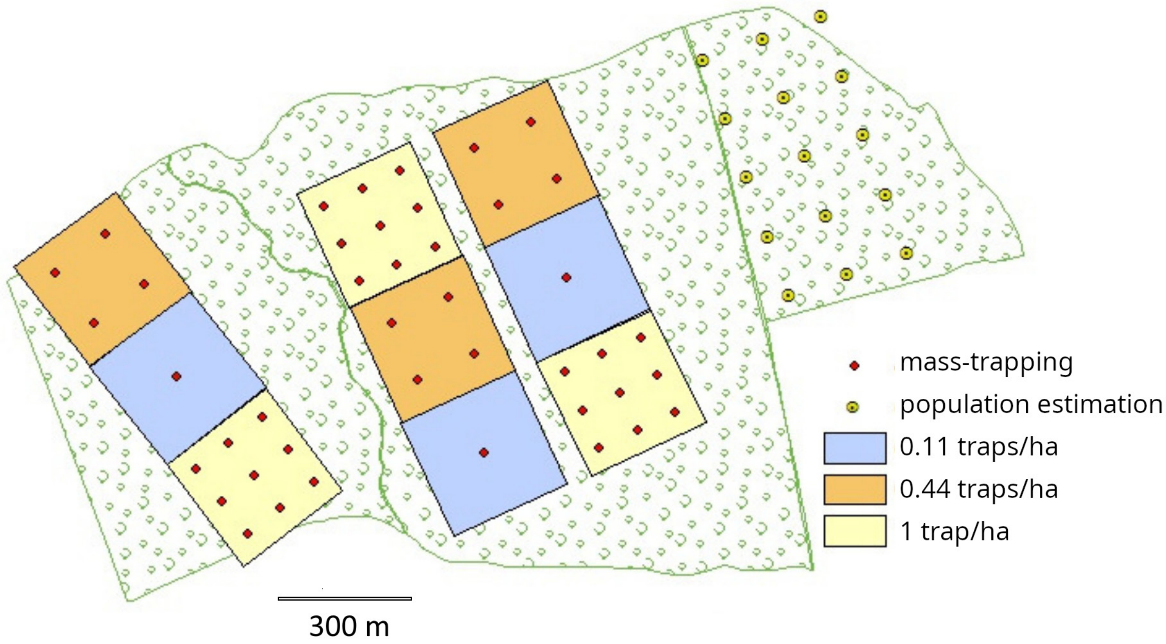

Figure 2. Layout of mass-trapping and population size estimation trials in Pino del Río (Palencia, Spain).

To evaluate the effectiveness of the mass-trapping method, three trapping densities were assessed considering the study on medium-high population densities conducted by Sánchez-Husillos et al. (2015): 0.11 traps/ha; 0.44 traps/ha and 1 trap/ha. Each treatment was deployed in a 9 ha square site in a randomized complete block design with three replications (Figure 2). Within each block, traps were distributed in such a way that they left a 50 m buffer between plots, and the blocks were separated by at least 60 m. The insects captured in the traps were sexed and removed from the assay. In addition, 217 previously identified insects (95 females and 122 males) were released as controls to validate the method. The insects used as controls were obtained from logs of *Pinus sylvestris* L. naturally colonized in Tabuyo del Monte (León), which were subsequently removed from the forest and transferred to an outdoor emergency cage located at the Calabazanos Forest Health Center dependencies. Newly emerged insects were identified, sexed, and measured for size and weight. These insects were subsequently released within two days of emergence and were identified using bee tags. Of these control insects, 127 were released at random points distributed throughout the population size estimation area, and 90 were released at random points distributed throughout the mass capture area. After catching them, they were released again between two consecutive traps to obtain useful information for the population size estimation trial, although for the mass-trapping efficiency assay, their capture was only considered once.

2.2. Mass-trapping campaigns in the area affected by the PWD

2.2.1. Study site

The study was carried out within the demarcated area officially established after PWN was first detected in the municipality of Sancti-Spíritus (Salamanca province, Castile and León, Spain) on 22 November 2013. Following this detection, the National Pine Wilt Nematode Contingency Plan and the corresponding regional plan for Castile and León were both activated.

A containment zone measuring approximately 55 km by 12 km was then delineated. Within this zone, a comprehensive management protocol was implemented. This included removing and analysing all declining pines and deploying an extensive network of pheromone-baited traps to monitor and capture *M. galloprovincialis*.

The data for this study were obtained from the official mass-trapping programme. The dataset covers the period from 2014 to 2023 and consists of records from two specific locations within the demarcated area: MUP-120 and a cluster of forests known as the 'La Gloria' public utility forests (Ciudad Rodrigo, Spain) (Figure 1). Both sites consist of mixed stands of 40-year-old *P. pinaster* and *Quercus ilex* (L., 1753) covering 779 and 236 ha, respectively.

2.2.2. Experimental design

Both Twelve-funnel Multi-funnel® traps and Crosstrap® (ECONEX S.L., Murcia, Spain) were used. Traps were hung from poles with the collection cup placed at least 50 cm from the ground. Traps were baited with Galloprotect 2D® lures (SEDQ S. L., Barcelona, Spain) that were replaced every six weeks. Table 1 shows the density of traps deployed and the annual insect catch recorded at each location. Additionally, wilted trees were removed from the forest to reduce the population of vectors by removing trees before they emerged. Both the removed trees and captured insects were tested for the presence of PWN.

Table 1. Density of traps, *Monochamus galloprovincialis* captures and wilted removed trees in Sancti-Spiritus managed areas (Salamanca, Spain)

Location	2014	2015	2016	2017	2018	2019	2020	2021	2022	2023
La Gloria 236 ha										
traps/ha	0.12	0.12	0.26	0.26	0.26	0.26	0.26	0.26	0.13	0.13
insect catches	1701	760	958	461	445	317	223	513	399	3479
wilted removed trees	148	121	30	62	56	55	55	10	54	139
MUP-120 779 ha										
traps/ha	0.12	0.12	0.19	0.19	0.19	0.19	0.19	0.19	0.10	0.10
insect catches	7251	2486	1844	1057	1425	1000	709	1611	1510	9696
wilted removed trees	471	448	239	180	280	252	262	59	352	300

2.3. Statistics

2.3.1. Population size estimation assay

Population size estimation in Pino del Río was carried out using the RMark package for R (Laake, 2013), following the Jolly-Seber methodology under POPAN parameterization. This assumes that the *M. galloprovincialis* population during the sampling periods was of the open type; therefore, birth, death, immigration, and emigration occurring during the trial were considered. Following this methodology, three primary parameters can be estimated: ϕi, the apparent survival probability (true survival minus permanent emigration) between occasions i and i + 1; pi, the probability of capture at occasion i; and penti, the probability that an individual from the superpopulation enters the population available for capture between occasions i and i + 1. This entry parameter encompasses both recruitment through adult emergence and immigration into the study area. From these primary parameters, three derived parameters are obtained: the population size (Ni) at each sampling interval, the number of new entries (Bi) between sampling occasions, and the total superpopulation size (ŇTot), which represents all individuals that were potentially available for capture at some point during the entire study period.

All possible models that considered time and sex in the probability of capture and survival were used. The best models were selected using the quasi-Akaike information criterion (AICc) (Lebreton et al., 1992). All models assumed equal probability of capture between marked and unmarked individuals, homogeneity of survival, correct marking of individuals, and immediate release after sampling. In addition, a second range of models was fitted in the case of insects released from the laboratory, but the parameter B_i was set to zero, considering that there were no new individuals entering the overpopulation during the experiment.

2.3.2. Mass-trapping assay

The total number of individuals in the population, ŇTot, had to be transformed into density units (D), which required fixing the area in which the insects were found. For a conservative approach, the total area sampled in this study was used. For the analysis of variance, the cumulative catches/trap and block factors were fitted to a Generalized Linear Model (GLM) with a Poisson error distribution. A Tukey HSD test with Bonferroni adjustment ($\alpha = 0.05$) was used to separate the mean cumulative catches/trap density and mean catches/trap in each treatment.

The regression between the trapping densities and removal proportions achieved by mass trapping was fitted to the GLM assumptions and a quasi-binomial error distribution to account for overdispersion. The trap densities at which 50% and 95% of the population could be removed were calculated using the fitted GLM.

2.3.3. Mass-trapping campaigns in the area affected by the PWD

Data from mass trapping campaigns in the MUP-120 and La Gloria Public Utility forests were analyzed independently using generalized linear mixed models with the GLIMMIX procedure in SAS software (SAS Institute Inc., 2023). Because the mass-trapping campaigns were not intended as a scientific trial and other issues, such as efficiency and work capacity were prioritized, the traps were not located in the same positions every year, nor was the same number of traps used throughout the time series. To facilitate data analysis, a 10 ha square grid cell was established, considering each grid cell as an experimental unit, with the sum of the annual captures of the traps contained within it as the response variable, and the number of traps contained in each cell as a measure of sampling effort. The model was adjusted based on the year, sampling effort, and number of wilted trees felled each year in each cell as fixed effects. The identity of each cell was incorporated as a random effect with a first-order heteroscedastic autoregressive covariance structure to adequately model temporal correlations within each cell. A Poisson distribution with a logarithmic link function was used given the nature of the response variable and goodness-of-fit criteria, and the model parameters were estimated using the maximum likelihood method.

3. RESULTS

3.1. Population size estimation

Only 14 individuals were captured in the population size estimation area, representing 11.7% of the insects released in this area (nine females and five males), whereas 47 individuals were recaptured in the mass capture area, which was 52.2% of the 90 released insects. Thus, it was found that the recaptures in the population size estimation area were not sufficient to estimate a model with an admissible error; therefore, only 47 captures of the 'mass-trapping area' were used in the estimation of released insects, whereas recaptures from all traps were used to estimate the native population.

The best fit of the Jolly-Seber models for laboratory-released insects showed that the probability of survival (ϕ) was time-dependent (Table 2), while the probability of capture (p) depended on the interaction of sex and time. Both parameters were fitted with an entry probability (pent) fixed at zero, since no new recruitment was expected from this closed group of released individuals, and population size at the sampling interval (N) was estimated as constant from the data. In contrast, for native-captured insects, apparent survival probability depended on the interaction between sex and time, whereas the probability of entry (pent) was conditioned only by time, reflecting the continuous recruitment through adult emergences and potential immigration into the study area throughout the sampling period.

Table 2. Summary of the best-fitting Jolly-Seber models for both released control insects and native *Monochamus galloprovincialis*

Insect source	Released insects	Best model	Nº. P.	AICc	(ŇTot ±SE)		
					Female	Male	Both
Lab reared	34 male 56 female	ɸ (~Time)p(~Time*Sex)pent(~1) N(~1)	7	156.1	33±14	39±14	72
Native		ɸ (~Time*Sex)p(~1)pent(~Time) N(~1)	8	1,047.6	1153±12	1,135±113	2,287

ɸ: probability of survival; pent: probability of entry; N: population size in the sampling interval; p: probability of capture; Nº. P., number of parameters in the model; AICc: quasi-Akaike information criterion; ŇTot ± SE: estimated population sizes. Estimates are derived from the weighted average parameters of the best models (ΔAICc < 10).

Although the estimated population size obtained for the control insects (72) subestimates the real value (90), it is within the range of the average ± the error standard: 33 ± 14 females and 39 ± 14 males; therefore, the precision of the estimates derived from the test was considered correct. By weighting the results of the best models (ΔAICc < 10), a superpopulation (ŇTot) of 2,287 native individuals was obtained for the entire study area (219 ha), resulting in a density of 10.94 insects/ha. Of these, 631 were captured once, and 78 were captured at least twice. Figure 3 shows the temporally predicted distribution of the local *M. galloprovincialis* population throughout the adult flight period in the Pino del Río area. Although males and females emerged in the same proportion, their curves soon diverged, with a higher proportion of males than females remaining at the end. Both sexes appeared to reach maximum local population size during the second week of August. After this, there was a decrease in population size, with more males than females. The average maximum flight distance estimated according to the models obtained was 348.51 m, which was very close to the average distance obtained between consecutive capture locations (309.78 m).

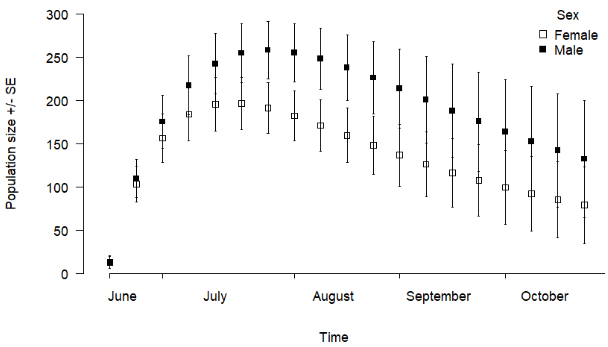

Figure 3. *Monochamus galloprovincialis* population size estimates by sexes per week in Pino del Río (Palencia, Spain).

3.2. Mass-trapping assay

A total of 512 native *M. galloprovincialis* (235 females, 277 males) were captured during the entire trapping period in the mass-trapping area of the Pino del Río assay. Weekly population size estimates obtained under POPAN parameterization were transformed to densities and were used to calculate the population removal percentages during the sampling period Significant differences in accumulated mean catches per trap were found between different trapping density sites, with the lowest density sites (0.11 traps/ha and 0.44 traps/ha) yielding the highest catches (19.0 and 15.3 catches/trap, respectively). These treatments showed significantly higher capture rates per trap compared to the highest density treatment 1 trap/ha (9.4 catches/trap; $p < 0.001$, Tukey test with Bonferroni correction), although no significant differences were detected between them ($p = 0.451$) (Figure 4a). However, the highest captures per hectare were obtained at higher densities (0.44 traps/ha and 1 trap/ha) with 7.37 and 9.41 catches/ha, respectively. These treatments showed significantly higher capture rates compared to treatment 0.11 traps/ha (2.11 catches/ha; $p < 0.05$, Tukey test with Bonferroni correction), although no significant differences were detected between them ($p = 1.000$) (Figure 4b).

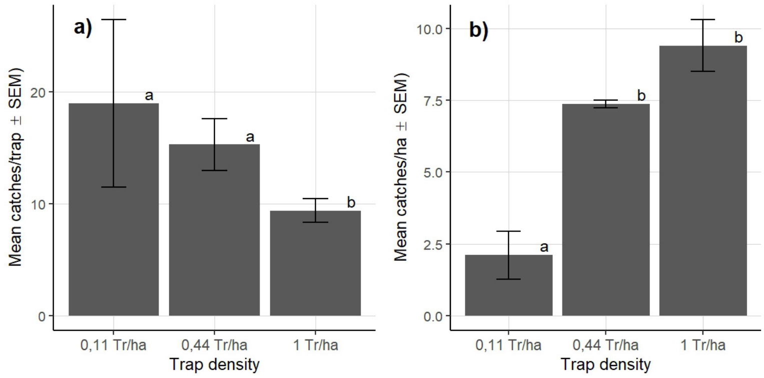

Figure 4. Mean of *Monochamus galloprovincialis* captures per trap (a) and per hectare (b) at different trap densities. Mean comparisons found using Tukey's HSD test with Bonferroni adjustment ($\alpha = 0.05$) after GLM Poisson ($n = 3$ replicates per density). Pino del Rio (Palencia, Spain).

Once the population size estimate had been converted into a density measure, the proportion of the *M. galloprovincialis* population removed by trapping was calculated. It was found that trapping densities of 0.11, 0.44 and 1 trap/ha removed 19.3%, 67.4% and 85% of the population, respectively. From these data, a logistic curve was calculated, relating the trapping density to the proportion of the population removed by trapping (Figure 5). As trapping intensity increased, a higher proportion of the local population was removed. The computation of the TD50 and TD95 values — the trap densities required to remove 50% and 95% of the estimated population in the sampling plot — forecasted values of 0.39 ± 0.12 SE traps/ha and 1.20 ± 0.34 SE traps/ha, respectively.

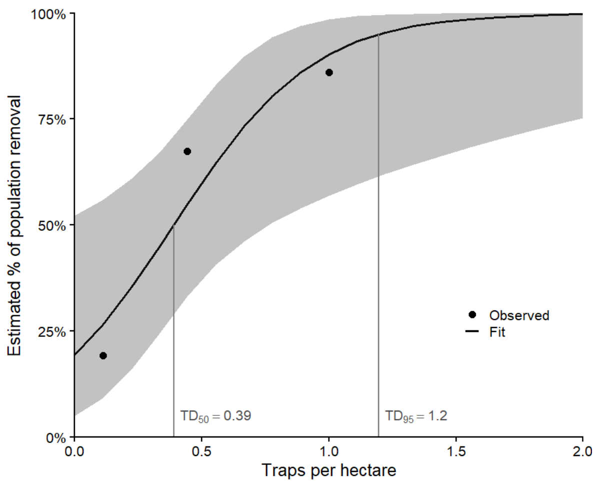

Figure 5. Logistic regression models fitted using quasibinomial generalized linear models (GLMs) with logit link relating trap density to the estimated proportion of Monochamus galloprovincialis population removed under low-density scenario (10.94 individuals/ha). Shaded area represents approximate 95% confidence interval. Estimated TD50 and TD95 values of traps per hectare required to remove 50% and 95% of the local populations are presented.

3.3. Mass-trapping campaigns in the area affected by the PWD

In both La Gloria and MUP-120 forests, catches increased in 2021 (Table 1), hampering the convergence of the intended models. Although the number of traps deployed in 2022 and 2023 was almost half that of previous years, the increase in *M. galloprovincialis* captures/trap was not solely due to this. Surveys for the control of the pine wood nematode carried out by the Regional Ministry of Environment, Housing and Land Planning (Consejería de Medio Ambiente, Vivienda y Ordenación del Territorio, Junta de Castilla y León) with the support of the Calabazanos Forest Health Center showed that it was a widespread phenomenon in trapping operations for this insect throughout the Castile and Leon region. This was likely due to tree stress from weather conditions, as 2022 and 2023 were exceptionally dry and hot years, providing a greater availability of colonizable material for insects. To facilitate model convergence, the data for 2022 and 2023 were considered unrepresentative of the effect of the variables to be adjusted and rejected, adjusting the models with the series from 2014 to 2021, both included.

In both locations, the fitted models showed that the sampling effort in each cell had a positive and highly significant effect on the predicted capture (Table 3). The number of trees felled did not have a significant effect, and its contribution to the model was marginal. Although a sufficiently high number of felling is expected to significantly influence the population captured the following year, not all symptomatic trees can be felled. This, combined with immigration processes typical of the open population, renders its effect undetectable in the current sampling design. The temporal variable exerted a highly significant effect in both locations revealing substantial differences in capture rates among years. The estimated mean captures showed a clear declining pattern consistent with progressive population depletion due to sustained mass trapping (Table 4). In La Gloria, mean captures declined from 7.21 insects/ha in 2014 to 0.94 insects/ha in 2020, representing a 87% reduction over the study period. Similarly, in MUP-120, captures decreased from 9.31 insects/ha in 2014 to 0.91 insects/ha in 2020, representing a 90% reduction. Post-hoc comparisons revealed that the first years of implementation (2014-2016) had significantly higher captures than the later years (2019-2020), demonstrating the cumulative effectiveness of continuous mass trapping (Table 4). The temporal autocorrelation parameter, ARH(1), was close to 1 in both cases (Table 3), indicating a strong dependence between consecutive years within each cell. This high autocorrelation suggests that cells with lower captures in one year tend to maintain low captures in the following year, reflecting the persistent local effect of mass trapping on reducing and maintaining low vector populations over time.

Table 3. Fitting parameters for log(captures/cell) of *Monochamus galloprovincialis* in Sancti-Spiritus-managed areas (Salamanca, Spain)

	Sampling effort				Removed trees				Year		ARH(1)	
Location	**Estimate**	**SE**	**t**	**p**	**Est.**	**SE**	**t**	**p**	**F**	**p**	**ρ**	**SE**
La Gloria	0.637	0.088	7.23	<0.0001	0.000	0.005	0.03	0.979	52.56	<0.0001	0.829	0.044
MUP-120	0.705	0.059	11.98	<0.0001	0.006	0.004	1.29	0.199	181.01	<0.0001	0.919	0.013

ARH(1): temporal correlation parameter.

The number of captures obtained at the beginning of the campaign, coupled with the abundance of decaying pines colonised by the insect, strongly suggested that both La Gloria and MUP-120 forests housed a very abundant insect population. Sánchez-Husillos et al. (2015) indicated that 0.37 and 0.82 traps per hectare would be needed to eliminate 50% and 95% of individuals, respectively, in a high-density population. Table 4 shows the captures predicted by our fitted model for La Gloria and MUP-120 forests (presented as captures/ha) for each year of the study campaign with sampling efforts of 0.37 and 0.82 traps/ha and no felled trees, since their effect on the fit is irrelevant. These estimates of 50% and 95% of the theoretical population and the surface areas of both forests (236 and 779 ha) allowed us to infer a range of native population densities. Based on the estimated native population densities and our field capture data, we estimated the proportion of the native population removed by mass trapping, ranging from a low of 1.27% for the most conservative option in 2014 to values exceeding 53%, just before the population begins to increase for other reasons, as previously discussed.

Table 4. Observed and estimated *Monochamus galloprovincialis* catches, estimated native population and estimated population removed for both La Gloria and MUP-120 mass trapping campaigns (Salamanca, Spain). Letters after Observed catches/ha indicate significantly different groups (Tukey test, α = 0.05)

	2014	2015	2016	2017	2018	2019	2020	2021
La Gloria, 0.37 traps/ha								
Observed catches/ha	7.21(a)	3.22(b)	4.06(b)	1.95(c)	1.89(c)	1.34(d)	0.94(e)	2.17(c)
Estimated catches/ha	30.80	11.33	6.30	2.56	2.52	1.85	1.14	3.33
Est. native population/ha	61.60	22.66	12.60	5.12	5.04	3.70	2.28	6.66
% removed pop.	**11.70**	**14.21**	**32.22**	**38.15**	**37.41**	**36.30**	**41.44**	**32.64**
La Gloria, 0.82 traps/ha								
Estimated catches/ha	538.56	198.18	110.15	44.80	44.07	32.45	20.07	57.73
Est. native population/ha	566.91	208.61	115.95	47.16	46.39	34.16	21.13	60.77
% removed pop.	**1.27**	**1.54**	**3.50**	**4.14**	**4.06**	**3.93**	**4.47**	**3.58**
MUP-120, 0.37 traps/ha								
Observed catches/ha	9.31(a)	3.19(b)	2.37(c)	1.36(e)	1.83(d)	1.28(e)	0.91(f)	2.07(d)
Estimated catches/ha	17.21	5.55	2.52	1.28	1.72	1.31	0.92	3.68
Est. native population/ha	34.42	11.10	5.04	2.56	3.44	2.62	1.84	7.36
% removed pop.	**27.04**	**28.75**	**46.97**	**53.00**	**53.18**	**49.00**	**49.46**	**28.10**
MUP-120, 0.82 traps/ha								
Estimated catches/ha	242.39	78.23	35.49	18.07	24.32	18.50	12.99	51.86
Est. native population/ha	255.15	82.35	37.36	19.02	25.60	19.47	13.67	54.59
% removed pop.	**3.65**	**3.88**	**6.34**	**7.13**	**7.15**	**6.59**	**6.66**	3.79

4. DISCUSSION

The application of the CMR method on *M. galloprovincialis,* supported by an efficient capture system of baited traps, allows for the evaluation of a direct control technique for insect vectors, such as mass capture. In addition, the efficient capture devices developed are very useful for other management methods, such as the early detection of disease or the inoculation of entomopathogens through self-dissemination techniques (Álvarez et al., 2015). In addition, the same trapping devices have been effective when applied to other *Monochamus* species in Europe and North America (Boone et al., 2018), favoring the possibility of introducing these techniques to other areas of potential new infestations.

Previous studies on the estimation of the population size of *M. galloprovincialis* fitted valid models for local populations considered to be of medium or high density in non-infested areas (82 individuals/ha) using Jolly-Seber models (Sánchez-Husillos et al., 2015). In our experiments in Pino del Río, a statistically valid result was obtained using the same methodology, but with populations considered to be of low density (10.94 individuals per hectare). The contrasting recapture rates observed between our population size estimation area (11.7% of released beetles) and the mass-trapping area (52.2%) provide important insights into the dynamics of open populations and the practical requirements of mark-recapture studies. This difference reflects the inherent characteristics of open populations, where dispersal, immigration, emigration, and mortality occur continuously during sampling periods—precisely the scenario for which the Jolly-Seber POPAN formulation was designed—. The lower recapture rate in the population size area is entirely consistent with the documented high dispersal capacity of

M. galloprovincialis. Previous studies have reported mean distances between consecutive captures of 518-680 m, with maximum distances exceeding 1,200 m (Sánchez-Husillos et al., 2015), demonstrating that in areas with sparse trap coverage, highly mobile beetles have substantial probability of dispersing beyond the trapping grid between sampling occasions.

The substantially higher recapture rate in the mass-trapping area directly demonstrates the positive relationship between trap density and capture probability (p_i), a key parameter in the Jolly-Seber model and central to understanding mass trapping effectiveness. The low number of laboratory-reared beetle recaptures in the population size estimation area (n = 14) proved insufficient for fitting models with admissible error, revealing a practical limitation inherent to mark-recapture methodologies: adequate sample sizes are necessary to generate statistically robust parameter estimates. This challenge is not unique to our study; Sánchez-Husillos et al. (2015) encountered similar difficulties with laboratory-reared beetles in their 2013 experiment, obtaining models with parameters that did not converge due to extremely low second-recapture numbers. Importantly, this limitation affected only the laboratory-reared beetle validation dataset and does not invalidate the native population estimates, which were based on sufficient recaptures across the entire study area and properly accounted for varying capture probabilities, survival rates, and recruitment patterns through the POPAN parameterization.

Shibata (1985) used the same Jolly-Seber methodology to study the relationship between *Monochamus alternatus* Hope, 1843 and PWD in infested areas, obtaining population densities as high as 1,176 individuals per hectare. Collectively, these results confirm that the Jolly-Seber model with POPAN parametrization is a valid and robust methodology for estimating the population density of *Monochamus* across a remarkable range of population densities—from approximately 11 individuals/ha in our low-density population to over 1,000 individuals/ha in PWD-affected areas—provided that sampling effort and trap density are adequate to obtain sufficient recaptures for reliable parameter estimation. The estimated results were consistent with the real ones, as was found for other saproxylic cerambycids (Tikkamäki & Komonen, 2011). The successful application of this methodology to low-density populations such as ours is particularly relevant for early detection and eradication programs in newly infested areas, where vector populations have not yet built up to high densities and where management interventions can be most cost-effective.

European legislation provides guidelines for eradication measures as a clear-cut of all susceptible hosts in a particular environment in case *B. xylophilus* infection is found. Owing to advances in the knowledge of insect dispersal capacity, the EU authorities have revised the clear-cutting radius over the last 10 years, from 3 km for the first outbreak in Spain (Villanueva de la Sierra, Cáceres) to the current minimum allowed of 100 m (European Commission, 2012). This strategy eliminates infested trees at an early stage of *B. xylophilus* introduction. However, as shown by other studies such as David et al. (2014) and Etxebeste et al. (2016), this will not be sufficient to prevent *Monochamus* beetles from dispersing from the delimited area to neighbouring forests because *M. galloprovincialis* is able to fly longer distances. This is also favored by habitat fragmentation, as observed after the large-scale eradication of felling (Gallego et al., 2012; Mas et al., 2013).

Therefore, it is necessary to develop new alternatives, such as mass trapping, to complement efforts to eradicate the disease in introduced areas. However, if resources are limited, management measures should be concentrated in areas where the largest population of vectors is found and, therefore, where the greatest risk of spreading PWN is present. This methodology could also be implemented on other continents with other *Monochamus* species because the trapping systems developed in Europe are effective for the detection of many exotic *Monochamus* species (Macias Samano et al., 2012; Pajares et al., 2013; Skabeikis et al., 2016).

The population extraction results obtained for the low-density population of Pino del Río (10.94 insects/ha) are consistent with those found by Sánchez-Husillos et al. (2015) for a medium/high-density population (82 insects/ha) (Figure 6). Our results show that there is an increase in catches per hectare as trapping intensity increases and this increase is not linear, but logistic, so that the corresponding adjusted logistic model predicts that a trapping density of 1.8 traps/ha would eliminate approximately 100% of a low-density population, while deploying only 0.82 traps/ha would result in a 90% reduction.

Sánchez-Husillos et al. (2015) obtained similar values for a population in medium/high density: 100% population eradication for a trapping intensity of 1.5 traps/ha and 95% extraction with an intensity of 0.82 traps/ha. This could mean that there is no density-dependent effect in the mass-trapping method for this insect at low and high densities, although it is not possible to predict what would happen in an epidemic level population where the nematode inoculations occur uncontrollably. In addition, it must be added that Togashi (1988) found a positive correlation between the proportion of weakened or killed trees and the average beetle density per tree in affected areas, in agreement with Yoshimura et al. (1999), that described the host–vector interaction between pines and pine sawyers carrying nematodes, which is directly correlated with the infestation level. These results demonstrate the possibility of using these methodologies to estimate population sizes to assess areas with the greatest potential risk and to choose the optimal trapping density based on the results that are deemed necessary. Both these results contribute significantly to disease control through the management of insect vectors.

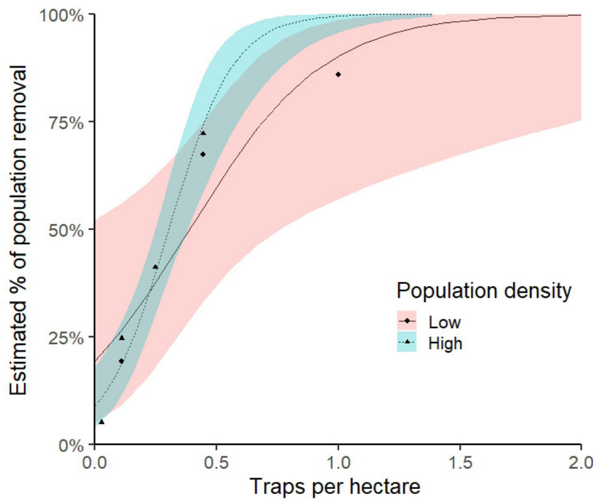

Figure 6. Logistic regression models fitted using quasibinomial generalized linear models (GLMs) with logit link relating trap density to the estimated proportion of *Monochamus galloprovincialis* population removed under low-density (10.94 individuals/ha) and high-density (82 individuals/ha) (Sánchez-Husillos et al., 2015) scenarios. Shaded areas represent approximate 95% confidence intervals

In the management of the La Gloria and MUP-120 stands in the demarcated area of Sancti Spiritus, mass trapping and felling of symptomatic trees have been implemented to control the disease, and experience confirms the effectiveness of this methodology. These were stands with a high risk of infection, high populations of *M. galloprovincialis*, and abundant trees with symptoms of decline colonized by the insect vector. Four years after the positive test in Sancti Spiritus, the disease was considered eradicated from the demarcated area. After 10 years of mass trapping and removal of symptomatic trees, no positive results have been found in the plant samples or vector insects analysis, while the stand remains healthy. The population of *M. galloprovincialis* and symptomatic trees, and therefore the probability of infection, have decreased dramatically. Although its effect has not been detected in the model, felling symptomatic trees is considered crucial in the management of the insect vector, since frequently, just one of these trees can give rise to more than 100 emerged insects (personal observation), which in the study forests has meant tens of thousands of individuals removed before emergence.

While our study successfully demonstrates the applicability of mark-recapture methodologies and mass trapping effectiveness at low population densities, several areas warrant further investigation. First, long-term monitoring studies comparing mass-trapping efficacy across multiple years and varying population densities would help elucidate whether density-dependent effects emerge at epidemic population levels, particularly in PWD-affected areas where uncontrolled nematode inoculations could drive exponential vector population growth. Second, research integrating spatial ecology approaches with CMR data—such as spatial capture-recapture (SCR) models—could provide more refined estimates of population density while explicitly accounting for spatial heterogeneity in detection probabilities and movement patterns. This would be particularly valuable for optimizing trap placement strategies in heterogeneous landscapes. Third, the interaction between habitat structure, forest management practices, and beetle dispersal behavior requires deeper investigation, as habitat fragmentation resulting from sanitation felling may paradoxically facilitate long-distance dispersal. Finally, the potential synergies between mass trapping and other control methods—such as biological control using entomopathogenic fungi—deserve systematic evaluation through controlled field experiments. These integrated approaches may offer more sustainable and cost-effective long-term solutions for PWD vector management.

Our results demonstrate that the development of new alternatives to clear-cutting, such as mass trapping and the removal of symptomatic trees, are effective and realistic options in environments where such measures would be counterproductive. However, if resources are limited or working conditions are challenging, e.g. due to rugged topography or severe weather, management measures should focus on areas with the highest vector populations, i.e. where the risk of PWN spread is greatest. This should not only apply to the distribution area of *M. galloprovincialis*, but also to other species in the genus.

Supplementary information ↑

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Supplementary material

Not applicable.

Data availability

Mass-trapping assay and population size estimation: The data supporting the findings of this study are available from the corresponding author upon reasonable request.

Mass-trapping campaigns in the area affected by the PWD: The data that support the findings of this study were provided by the Forest Health Centre of Calabazanos. Restrictions apply to the availability of these data, which were used under license for the current study, and so are not publicly available. Data are available from the authors upon reasonable request and with permission of the Regional Ministry of Environment, Housing and Spatial Planning, Regional Government of Castile and León. 34004 Palencia, Spain.

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Authorship contribution statement

Estela Sánchez-Husillos: Data curation, Investigation, Visualization, Writing – original draft.

Iñaki Etxebeste-Larrañaga: Data curation, Formal analysis, Software, Validation, Visualization.

Gonzalo Álvarez-Baz: Visualization, Writing – original draft, Writing – review & editing.

Ana B. Martín-Hernández: Methodology, Resources, Supervision.

Juan C. Domínguez Alonso: Methodology, Resources, Supervision.

Juan A. Pajares-Alonso: Conceptualization, Funding acquisition, Project administration, Supervision.

Competing interests

The authors have declared that no competing interests exist.

Statement on the use of Artificial Intelligence

Not applicable.

REFERENCES

Álvarez G, Gemeno C, 2022. In Memoriam. Juan Pajares (1959-2020). Cuad Soc Esp Cienc For 48: 25–34. https://doi.org/10.31167/csecfv0i48.19925

Álvarez G, Fernández-Bravo M, Pajares J, Quesada-Moraga E, 2015. Potential of native *Beauveria pseudobassiana* strain for biological control of Pine Wood Nematode vector *Monochamus galloprovincialis*. J Invertebr Pathol. 132: 48–56. https://doi.org/10.1016/j.jip.2015.08.006

Álvarez G, Gallego D, Hall DR, Jactel H, Pajares JA, 2016. Combining pheromone and kairomones for effective trapping of the pine sawyer beetle *Monochamus galloprovincialis*. J Appl Entomol. 140: 58–71. https://doi.org/10.1111/jen.12297

Álvarez G, Etxebeste I, Gallego D, David G, Bonifacio L, Jactel H, Sousa E, Pajares JA, 2014. Optimization of traps for live trapping of Pine Wood Nematode vector *Monochamus galloprovincialis*. J Appl Entomol. https://doi.org/10.1111/jen.12186

Boone C, Sweeney J, Silk P, Hughes C, Webster R, Stephen F, Maclauchlan L, Bentz B, Drumont A, Zhao B et al., 2018. *Monochamus* species from different continents can be effectively detected with the same trapping protocol. J Pest Sci 92. https://doi.org/10.1007/s10340-018-0954-4

Consejería de Agricultura y Desarrollo Rural, 2008a. *Resolución de 12 de noviembre de 2008, de la Dirección General de Explotaciones y Calidad Alimentaria, por la que se declara contaminada por el nematodo de la madera del pino Bursaphelenchus xylophilus (Steiner et Buhrer) Nickle et al. determinada área forestal del término municipal de Villanueva de la Sierra y se establece una zona demarcada de 20 kilómetros de radio, adoptándose en ella diversas medidas fitosanitarias tendentes al control y erradicación del agente patógeno.* Diario Oficial de Extremadura, nº 233, 2 de diciembre de 2008, pp. 32028–32036. (2008063666). https://doe.juntaex.es/pdfs/doe/2008/2330o/08063666.pdf

Consejería de Agricultura y Desarrollo Rural, 2008b. *Resolución de 20 de noviembre de 2008, de la Dirección General de Explotaciones Agrarias y Calidad Alimentaria, por la que se adopta la medida fitosanitaria consistente en la tala y destrucción de todas las plantas susceptibles situadas en el polígono de actuación especificado en el Anexo, con relación al foco contaminado por el nematodo de la madera del pino Bursaphelenchus xylophilus (Steiner et Buhrer) Nickle et al. en determinada área forestal del término municipal de Villanueva de la Sierra, previamente declarado por esta Dirección General.* Diario Oficial de Extremadura, nº 234, 3 de diciembre de 2008, pp. 32239–32242. (2008063675). https://doe.juntaex.es/pdfs/doe/2008/2340o/08063675.pdf

David G, Giffard B, Piou D, Jactel H, 2014. Dispersal capacity of *Monochamus galloprovincialis*, the European vector of the pine wood nematode, on flight mills. J Appl Entomol. 138: 566–576. https://doi.org/10.1111/jen.12110

Etxebeste I, Estela S-H, Alvarez G, Mas H, Pajares J, 2016. Dispersal of *Monochamus galloprovincialis* (Col.: Cerambycidae) as recorded by mark–release–recapture using pheromone traps. J Appl Entomol. 140: 485–499. https://doi.org/10.1111/jen.12278

European Commission, 2006. *Commission Decision 2006/133/EC of 13 February 2006 requiring Member States temporarily to take additional measures against the dissemination of Bursaphelenchus xylophilus (Steiner et Buhrer) Nickle et al. (the pine wood nematode) as regards areas in Portugal, other than those in which it is known not to occur.* Official Journal of the European Union, L 52, 34–36. https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX:32006D0133

European Commission, 2012. Commission Implementing Decision 2012/535/EU of 26 September 2012 on emergency measures to prevent the spread within the Union of Bursaphelenchus xylophilus (Steiner et Buhrer) Nickle et al. (the pine wood nematode) (notified under document C(2012) 6543). Official Journal of the European Union, L 266, 42–52, 27 September 2012. https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX%3A32012D0535

Evans HF, McNamara DG, Braasch H, Chadoeuf J, Magnusson C, 1996. Pest Risk Analysis (PRA) for the territories of the European Union (as PRA area) on *Bursaphelenchus xylophilus* and its vectors in the genus *Monochamus*. EPPO Bulletin. 26: 199–249. https://doi.org/10.1111/j.1365-2338.1996.tb00594.x

Gallego D, Sánchez-García F, Mas H, Campo M, Lencina JL, 2012. Estudio de la capacidad de vuelo a larga distancia de *Monochamus galloprovincialis* (Olivier 1795). (Coleoptera: Cerambycidae) en un mosaico agro-forestal. Boletín de Sanidad Vegetal -Plagas. 39: 109–123.

Laake JL, 2013. RMark: An R Interface for Analysis of Capture-Recapture Data with MARK. Alaska Fish. Sci. Cent., NOAA, Natl. Mar. Fish. Serv.: Seattle, WA https://apps-afsc.fisheries.noaa.gov/Publications/ProcRpt/PR2013-01.pdf.

Lebreton J-D, Burnham KP, Clobert J, Anderson DR, 1992. Modeling Survival and Testing Biological Hypotheses Using Marked Animals: A Unified Approach with Case Studies. Ecological Monographs. 62: 67–118. https://doi.org/10.2307/2937171

Linit MJ, Akbulut S, 2008. The Insect Vectors: Biology and Ecology, In: Pine wilt disease: A worldwide threat to forest ecosystems. Ed. by Mota MM, Vieira, PR, Springer Netherlands, pp. 211-213.

Macias Samano J, Wakarchuk D, Millar J, Hanks L, 2012. 2-Undecyloxy-1-ethanol in combination with other semiochemicals attracts three *Monochamus* species (Coleoptera: Cerambycidae) in British Columbia, Canada. Can Entomol. 144: 821–825.

Mas H, Hernández R, Villaroya M, Sánchez G, Pérez-Laorga E, González E, Ortiz A, Lencina JL, Rovira J, Marco M et al., 2013. Comportamiento de dispersión y capacidad de vuelo a larga distancia de *Monochamus galloprovincialis* (Olivier 1795). https://doi.org/10.13140/2.1.2707.5529.

Naves PM, Camacho S, De Sousa EM, Quartau JA, 2007. Transmission of the pine wood nematode *Bursaphelenchus xylophilus* through feeding activity of *Monochamus galloprovincialis* (Col., Cerambycidae). J Appl Entomol. 131: 21–25. https://doi.org/10.1111/j.1439-0418.2006.01111.x

Pajares J, Ibeas F, Diez J, Gallego D, 2004. Attractive reponses by *Monochamus galloprovincialis* (Col., Cerambycidae) to host and bark bettle semiochemicals. J Appl Entomol. 128: 633–638. https://doi.org/10.1111/j.1439-0418.2004.00899.x

Pajares JA, Álvarez G, Hall DR, Douglas P, Centeno F, Ibarra N, Schroeder M, Teale SA, Wang Z, Yan S et al., 2013. 2-(Undecyloxy)-ethanol is a major component of the male-produced aggregation pheromone of *Monochamus sutor*. Entomol Exp Appl. https://doi.org/10.1111/eea.12113

Sánchez-Husillos E, Etxebeste I, Pajares J, 2015. Effectiveness of mass trapping in the reduction of *Monochamus galloprovincialis* Olivier (Col.: Cerambycidae) populations. J Appl Entomol. 139. https://doi.org/10.1111/jen.12219

SAS Institute Inc., 2023. SAS/STAT® 15.3 User's Guide. SAS Institute Inc., Cary, NC: Cary, NC, USA.

Shibata E, 1985. Seasonal Fluctuation of the Pine Wood Nematode, *Bursaphelenchus xylophilus* (STEINER et BUHRER) NICKLE (Nematoda : Aphelenchoididae), Transmitted to Pine by the Japanese Pine Sawyer, *Monochamus alternatus* HOPE (Coleoptera : Cerambycidae). Appl Entomol Zool. 20: 241–245. https://doi.org/10.1303/aez.20.241

Skabeikis DD, Fierke MK, Teale SA, 2016. Field Response of *Monochamus scutellatus scutellatus* and *Monochamus notatus* (Coleoptera: Cerambycidae) to the Male-Produced Pheromone, 2-(Undecyloxy)-Ethanol, and Host Volatiles. J Econ Entomol. 109: 1220–1225.

Tikkamäki T, Komonen A, 2011. Estimating population characteristics of two saproxylic beetles: A mark-recapture approach. J Insect Conserv. 15: 401–408. https://doi.org/10.1007/s10841-010-9313-3

Togashi K, 1988. Population density of *Monochamus alternatus* adults (Coleoptera: Cerambycidae) and incidence of pine wilt disease caused by *Bursaphelenchus xylophilus* (Nematoda: Aphelenchoididae). Popul Ecol. 30: 177–192. https://doi.org/10.1007/BF02513243

Torres-Vila LM, Zugasti C, De-Juan JM, Oliva MJ, Montero C, Mendiola FJ, Conejo Y, Sánchez A, Fernández F, Ponce F et al., 2014. Mark-recapture of *Monochamus galloprovincialis* with semiochemical-baited traps: Population density, attraction distance, flight behaviour and mass trapping efficiency. Forestry. 88: 224–236. https://doi.org/10.1093/forestry/cpu049

Vives E, Ramos MA, 2000. Fauna Iberica. vol. 12, Coleoptera, Cerambycidae. Museo Nacional de Ciencias Naturales y Consejo Superior de Investigaciones Cientificas.

Wingfield M, 1982. Association of Pine Wood nematode with stressed trees in Minnesota, Iowa, and Wisconsin. Plant Disease. 66: 934.

Wingfield M, Blanchette R, 1983. The pine-wood nematode, *Bursaphelenchus xylophilus*, in Minnesota and Wisconsin: Insect associates and transmission studies. Can J For Res. 13: 1068–1076.

Yoshimura A, Kawasaki K, Takasu F, Togashi K, Futai K, Shigesada N, 1999. Modeling the Spread of Pine Wilt Disease Caused by Nematodes with Pine Sawyers as Vector. Ecology. 80: 1691–1702. https://doi.org/10.1890/0012-9658(1999)080[1691:MTSOPW]2.0.CO;2